# Predormancy omnivory in European cave bears evidenced by a dental microwear analysis of *Ursus spelaeus* from Goyet, Belgium

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**Previous morphological and isotopic studies indicate that Late Pleistocene cave bear (*Ursus spelaeus*) diet ranged from mostly vegetarian to omnivory or even carnivory. However, such analyses do not provide information on seasonal diets, and only provide an average record of diet. A dental microwear analysis of 43 young and adult individuals demonstrate that, during the predormancy period, cave bears from Goyet (Late Pleistocene, Belgium) were not strictly herbivorous, but had a mixed diet composed of hard items (e.g., possibly bone), invertebrates (e.g., insects), meat (ungulates, small vertebrates), and/or plant matter (hard mast, seeds, herbaceous vegetations, and fruits). Therefore, our results indicate that cave bears at Goyet were generalist omnivores during the predormancy period, which is consistent with current data on the dietary ecology of extant bears during this season. These data also raise questions about the ecological role and causes of the extinction of cave bears.**

dormancy | Pleistocene | Carnivora | Ursidae | ecology

Late Pleistocene caves of Europe have yielded abundant fossils of the cave bear *Ursus spelaeus*, an extinct close relative of the brown bear, *Ursus arctos*, and the polar bear, *Ursus maritimus* (1–4). It is one of the best known extinct mammals, and demographic and stable isotopes analyses have shown them to have had a metabolism similar to that of extant bears. In particular, they went through a period of dormancy during the winter, giving birth and nursing their offspring during the dormancy, and maintained their body temperature without defecating or urinating, eating or drinking (5–8). Cave bear diet is more controversial. Dental traits (enlarged and multicusped molars, loss of the three anterior premolars, molarization of the fourth upper premolars, and rapidly occurring wear on the cheekteeth) suggest that cave bears fed on abrasive food (presumably plants) and were more engaged in herbivory than the other bear species (5, 9–11). Skull and mandible morphology of cave bears was interpreted in a similar way (12), but recently, it has been shown to correlate with omnivory or even carnivory among bears (13), which was supported by taphonomical evidence (11, 14, 15). Nitrogen stable isotopes ($^{15}N/^{14}N$ or $\delta^{15}N$) in bone collagen of adult cave bears from well dated sites with comparative mammalian data indicate a dietary range from vegetarianism (16–19) to omnivory (20).

Nutritional ecology of North American extant bears (polar bears excluded) indicates that they are generalist omnivores, yet their diets range from almost complete vegetarianism to carnivory depending on season, habitat, sex, and/or foraging behavior (12, 21–25). However, similar information on the variation of cave bear diet through time has rarely been provided. Short-term (annual, seasonal) variation has no impact on tooth or skull shape, and bone collagen, due to slow turnover (ref. 26, and references therein, and ref. 27), provides a record of the diet averaged over several years or a lifetime (8, 28). Therefore, finer resolution is necessary to sort out the dietary dynamics of cave bears. Finer resolution is also fundamental to assess the paleoecology of this animal, its impact on the environment, its relationships with coeval large mammals, and, last, to understand the causes of its extinction.

To provide a perspective on seasonal variation in cave bear diet, we analyzed the dental microwear pattern of cave bears from three Late Pleistocene horizons of Goyet, Belgium (*SI Materials and Methods*) (29–33). Dental microwear analysis quantifies and compares different types of dental microwear resulting from processing food during the meals of the previous few days (34). This method has long been used to reconstruct the diet of fossil primates and ungulates (35, 36), and has proven to be informative for fossil carnivores (37, 38). Because cave bear remains usually accumulate in caves as a result of deaths during hibernation (5, 7), dental microwear analysis provides a unique opportunity to access bears' diet immediately before they go into dormancy.

## Results

Regarding microwear pattern of *U. spelaeus* from Goyet, all of the cave bear specimens studied here display many of microwear features (Table 1). We did not observe any obliteration of microwear features resulting from a high oral acidity during dormancy, which was suggested in a previous study of dental microwear in cave bears (39) to explain the absence of microwear features. Because this pattern is well known in extant carnivores (e.g., hyaenids), it is easily identifiable (38).

Fig. 1 displays the distribution of extant species clustered in dietary categories and samples of *U. spelaeus* through a principal component analysis (PCA) (Table S1), using four independent variables of dental microwear and 178 specimens representing 17 extant species nested in nine diet categories (Table 1; Table S2). The cave bear samples were then added as supplementary data. According to the Kaiser' criterion, the drop in percentage of the

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**Table 1. Statistical summary of dental microwear pattern for extant species clustered in diet categories and samples of *U. spelaeus***

| | | Nws | | Nlp | | Nfs | | Nsp | |
|---|---|---|---|---|---|---|---|---|---|
| | *N* | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| Extant species in diet categories | | | | | | | | | |
| Meat-eaters | 40 | 4.7 | 2.4 | 47.1 | 30.0 | 14.2 | 3.8 | 227.1 | 95.0 |
| Bone-eaters | 19 | 7.4 | 3.4 | 40.2 | 11.6 | 16.8 | 4.8 | 100.7 | 31.0 |
| Herbivores | 5 | 5.8 | 2.5 | 15.0 | 7.0 | 54.6 | 8.9 | 89.2 | 43.3 |
| Fruit-eaters | 11 | 9.5 | 2.6 | 42.4 | 12.8 | 24.4 | 11.5 | 246.9 | 88.4 |
| Insect-eaters | 30 | 5.9 | 3.3 | 37.6 | 10.0 | 16.4 | 5.4 | 219.5 | 43.8 |
| Worm/larvae-eaters | 7 | 6.7 | 1.9 | 33.7 | 6.8 | 32.6 | 4.3 | 77.7 | 17.4 |
| Malacophages | 4 | 7.0 | 1.6 | 25.5 | 12.2 | 16.5 | 2.4 | 76.0 | 21.1 |
| Omnivores | 42 | 8.4 | 3.0 | 37.6 | 12.9 | 21.0 | 9.4 | 179.8 | 62.3 |
| Fish-eaters | 20 | 5.4 | 3.2 | 69.8 | 14.8 | 19.7 | 4.6 | 366.8 | 82.1 |
| *U. spelaeus* both age classes/all horizons | 43 | 4.5 | 2.2 | 28.3 | 9.3 | 33.6 | 7.4 | 160.7 | 44.3 |
| Adults/horizon 3 | 5 | 5.2 | 0.8 | 24.0 | 6.5 | 29.6 | 7.5 | 160.4 | 16.1 |
| Adults/horizon 4 | 4 | 7.0 | 1.4 | 40.8 | 5.9 | 30.5 | 4.4 | 167.8 | 19.2 |
| Adults/horizon 5 | 5 | 5.0 | 3.1 | 26.0 | 11.2 | 37.4 | 3.9 | 138.2 | 50.6 |
| Juveniles/horizon 3 | 11 | 3.4 | 1.7 | 25.3 | 5.8 | 32.8 | 7.1 | 192.7 | 42.1 |
| Juveniles/horizon 4 | 9 | 5.2 | 2.5 | 24.6 | 9.2 | 29.8 | 8.5 | 135.7 | 46.3 |
| Juveniles/horizon 5 | 9 | 3.3 | 1.7 | 34.0 | 8.6 | 35.1 | 8.3 | 156.0 | 43.6 |

For list of extant and extinct specimens, see Tables S2 and S4. *N*, sample size.

total variance expressed from the third to the last eigenvalue allow us to disregard coordinates from the fourth component (40).

Along the first axis (47.5% of the total variance), the distribution of extant specimens is mainly affected by a negative association with the number of small (Nsp) and large pits (Nlp) (Fig. 1; Table S1). Fish-eaters with low coordinates are characterized by a more intense pitting than other species. Herbivores with low pitting represent the cluster with the highest coordinates. *U. spelaeus* shows an intermediate Nsp and Nlp, differs from both fish-eaters and herbivores, and plots with dietary categories that form a central cluster along this axis. In this aspect, cave bears were most similar to omnivores, bone-eaters, worm/larvae-eaters, and malacophages (Fig. 1 and Table 1).

Along the second axis (23.1% of the total variance), the distribution of extant specimens is mainly controlled by the positive weight of the number of wide scratches (Nws) (Fig. 1; Table S1). Herbivores have the smallest Nws, and the fruit-eaters have the largest Nws. Cave bears are located between herbivores and other dietary categories, in particular worm/larvae-, meat-, and insect-eaters.

Along the third axis (21.0% of the total variance), the distribution of extant specimens is mainly due to the negative weight of the number of fine scratches (Nfs) (Fig. 1; Table S1). Herbivores have high Nfs values; all of the other categories differ from Herbivores in having a fewer Nfs, and especially from meat-, bone-, insect-eaters, and malacophages. *U. spelaeus* are located close to fish-, fruit-, and worm/larvae-eaters.

The distribution of the cave bears throughout the PCA does not support any dietary specialization. Their dental microwear is distinctly separate from that of a strict vegetarian diet (based either on fruits and/or foliage). Instead, the dental microwear pattern suggests that cave bears had a broad dietary spectrum.

The distribution of *U. spelaeus* from Goyet did not reveal any associations between stratigraphical origin (horizon 3, 4, or 5) or relative age (juveniles versus adults) and their dental microwear patterns (Fig. 1, Table 1). With the exception of the adults from horizon 4 that are located closer to meat-, insect-, worm/larvae-eaters, malacophages along the second axis of the plot, all subsamples of *U. spelaeus* are grouped around the average coordinates of the species.

## Discussion

Our analysis supports the hypothesis that, at least before dormancy, cave bears from Goyet were not specialized, but rather had a mixed diet based on meat (ungulates, small vertebrates), plant matter (hard mast, seeds, herbaceous vegetations, and fruits), hard items (possibly bone), and invertebrates (insects, worm/larvae), although the proportion of each of those categories cannot be determined.

The absence of differences in the microwear patterns of adult and young bears indicates that they fed on similar food items. This result agrees with previous hypotheses that, although young cave bears received milk during their first two winters, they fed on solid food during their first summer (9, 28), and had access to the same food sources as adults during their first fall. The absence of notable microwear pattern differences between individuals with regard to their stratigraphic location suggests that cave bears kept similar predormancy feeding preferences over the occupation of the cave.

The predormancy dietary ecology of extant, temperate-zone bears (i.e., the brown bear, *U. arctos*, and the American black bear, *U. americanus*, for which nutritional data are the most complete) is, therefore, relevant to the interpretation of cave bear dental microwear. Between summer and fall, extant bears gain body mass by hyperphagia and accumulate fat to face the costs of dormancy and, in the case of females, reproduction and lactation (41–44). This gain results from a balance between energy expenditure, intake, foraging time, and fat accumulation, depending primarily on availability, foraging efficiency, body size, and condition (45, 46). As a result, a mixed diet is the most common one in extant bears in the fall, which may include one dominant item such as terrestrial vertebrates (mostly ungulates and rodents) (47–50), insects (especially ants) (51), roots (52), berries (50, 52), or hard mast (53). Dietary specialization, based on a single food source, in extant bears is unlikely in the fall. Thus, although strict herbivory in extant bears is well documented in the spring and early summer, this specialization does not happen in the fall before dormancy (50, 51, 54). Also, because foraging efficiencies increasingly constrain growth rates, only small extant bears (<120 kg) can gain weight from foraging heavily on plants (berries or herbaceous vegetation) (54, 55). That cave bears were comparable in size with the largest extant ursids (56) suggests that they were not able to gain weight from an exclusively vegetarian diet before dormancy.

By using the ratios of nitrogen stable isotopes from hair (annual assimilated diet) and underfur or hair sections (autumn assimilated diet) to analyze assimilated diet, meat was shown to

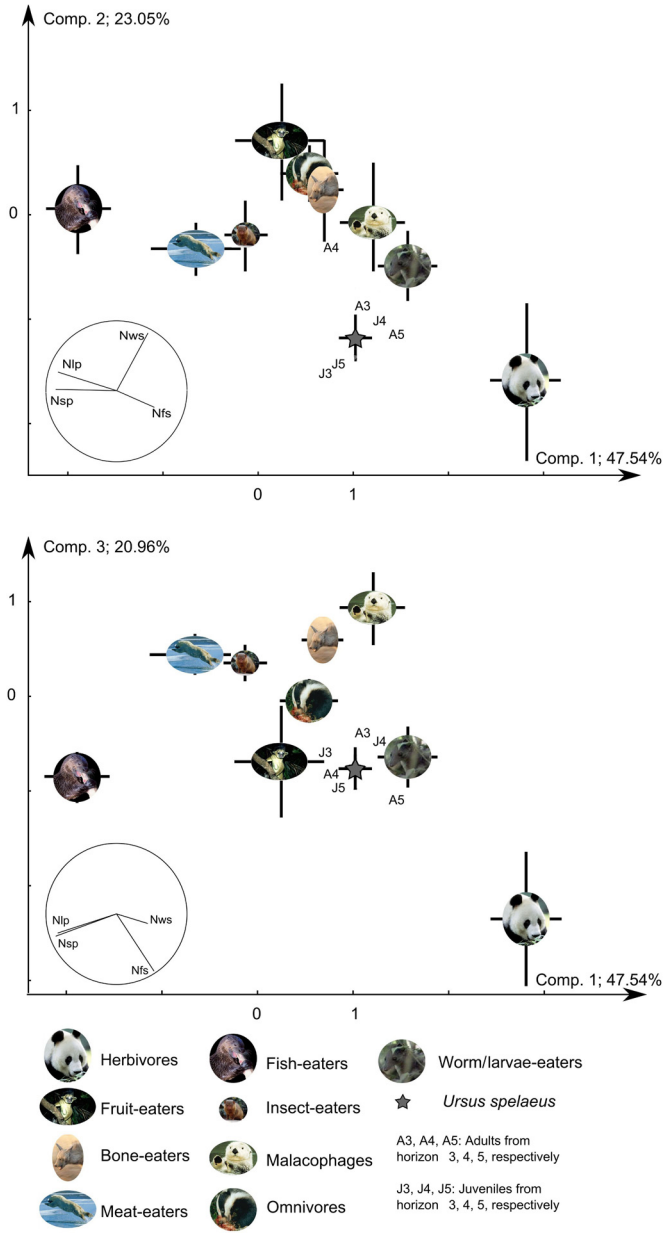


**Fig. 1.** Principal component analysis. One hundred seventy-eight specimens representing 17 extant species were clustered in diet categories and four independent variables (Nfs, Nws, Nsp, and Nlp) in the PCA framework; fossil samples were used as supplementary data.

positively affect body size in extant bears when abundant (57) and to be an important contribution to the fall assimilated diet of grizzly bears (23). However, there is a limit to how much protein-rich food bears want to consume (45, 46), which indicates that cave bears were probably not strictly carnivorous during the predormancy period. The other food categories inferred from dental microwear analysis for the diet of cave bears from Goyet are never frequent in extant bear diet. Similarities observed in the dental microwear patterns between some cave bear individuals from Goyet and the worm/larvae eaters probably result from foraging activities on the ground that may imply grubbing for roots or rodents in addition to grit/soil ingestion, as in extant worm/larvae eaters (38) and in extant bears (51); consumption of larvae and/or earthworms by extant bears is relatively rare and occurs mainly in the spring (58). Consumption of bones or marrow is not documented in extant bears, although it has been suggested for extinct species such as *Arctodus simus* (59) and some populations of *U. spelaeus* (14, 15, 39). Extant durophagous species (e.g., hyaenids, sea otter) that consume hard items have a high percentage of wide scratches and large pits (38). These percentages are lower in our cave bear samples. Although bone consumption may have existed at Goyet (Fig. 1), it was not frequent.

## Conclusions

Dental microwear analysis of the cave bears from Goyet demonstrates that, at least during the predormancy period, their diet included a great variety of food items, including protein-rich items such as meat and high-energy items such as berries. Given their large body size and nutritional requirements before dormancy, this result is consistent with the dietary ecology of extant, temperate-zone bears. This dietary flexibility raises questions as to the ecological role within the ecosystems and causes of the extinction of this species. Pacher and Stuart (11) concluded that cave bear extinction was probably due to a marked deterioration in quantity and quality of available plant food, a hypothesis resulting from the belief that cave bears were largely herbivorous. However, our results point out that it is necessary to more precisely portray the dietary ecology of cave bears before proposing hypotheses about their extinction. By providing some perspective on seasonal variation, dental microwear analysis proves to be a powerful tool, along with morphology and stable isotopes on bone collagen, to sort out the dietary dynamics of cave bears.

## Materials and Methods

**Cave Bear Sample from Goyet.** The cave bear material analyzed here comes from chamber A and B of the Goyet cave, and principally from chamber B. Five horizons were defined in the cave, but specimens used here come from horizons 3, 4, and 5 of chamber A or B (see *SI Materials and Methods* and Figs. S1 and S2). Accelerator mass spectrometry (AMS) radiocarbon ages of the carnivore assemblages from the three horizons provided ages of carnivores cave occupation that ranged from ≈41 to 32 cal kyr BP (Table S3). The material used for dental microwear analyses included lower carnassials of 43 juvenile (erupting permanent dentition) and adult (fully erupted permanent dentition) individuals of both sexes (Table S4). All of the juveniles were individuals that died during their second hibernation. The individuals from Goyet were identified as *U. spelaeus*, not *U. arctos*, based on their size and morphology. Thus, the carnassials had a mean crown length of 29.8 mm (60), with a very developed protoconid, and a metaconid that was generally composed of two large cuspids, as was the entoconid. Only a few lower carnassials from *U. arctos* could be recognized from Goyet, and they all had a mean crown length of ≈23 mm (32).

**Dental Microwear and Database.** The comparative database used here is described in detail in Goillot et al. (38). It includes 178 individuals representing 17 extant species belonging to 10 different families of the order Carnivora. These species are clustered in distinct dietary specializations: omnivores (two species), meat-eaters (three species), bone-eaters (two species), a fish-eater, herbivores (two species), a worm/larvae eater, insect-eaters (three species), fruit-eaters (two species), and one malacophage (for the species and a list of the specimens, see Table S2). The Ursidae are represented by *U. maritimus*, *A. melanoleuca*, *Melursus ursinus*, and *Tremarctos ornatus*.

The use of optical stereomicroscopy to analyze microwear patterns on enamel surface is noninvasive and precise. Also, Merceron et al. (61, 62) improved the reproducibility of this technique substantially. Goillot et al. (38) applied this method to a large sample of extant carnivores and demonstrated that analyzing the carnassials' slicing facet is the best way of inferring the diet of carnivores. They also pointed out that the selected area on each facet is representative of the whole facet, and that the differences between species do not reflect phylogenetic relationships, but feeding habits. The procedure of molding described by Merceron et al. (61, 62) and the image processing and acquisition of data described in Goillot et al. (38) were applied here, using the same instruments. The slicing facets used to study microwear features (pits and scratches) were the labial facet of m1 paraconid (when the m1 facet is unavailable or poorly preserved, its analogous facet on P4, the distolingual facet of the metacone, is used) (38).

A 300-$\mu$m side square (0.09 mm$^2$) was analyzed on the photograph of each facet. The dimensions of this square allowed the analysis of the facets of the smallest extant and extinct taxa among carnivores. The variables measured were: Nws, breadth $>5$ $\mu$m; Nlp, major axis $>5$ $\mu$m; Nfs, breadth $<5$ $\mu$m; and Nsp, major axis $<5$ $\mu$m (38).

Differences between *U. spelaeus* and extant species clustered in diet categories were investigated through a PCA using Statistica, version 7. Extant specimens were used in the PCA with the four independent variables: Nws, Nfs, Nsp, and Nlp. The samples of *U. spelaeus* were then used as supplementary data, and therefore, do not affect the PCA framework initially based on extant specimens.

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